



ORIGINAL ARTICLE

Diversity patterns of bivalves in a coral dominated shallow-water bay in the northern Red Sea – high species richness on a local scale

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Abstract

Bivalve species richness in the Northern Bay of Safaga, northern Red Sea, was assessed through original collecting activity in water depths from the intertidal to >50 m and by incorporating selected literature records. One-hundred-and-ninety-three samples, yielding 16,320 shells (dead and living), were taken from a coral-dominated coastal area that covers approximately 75 km². Two-hundred-and-forty-three bivalve species were recognized; this is the highest number of species reported to date for any coastal area of comparable size. This high species richness can be related to the great habitat variety in the bay and the major sampling effort, including quantitative and qualitative samples from hard and soft substrata, which enabled us to detect many rare species. Species accumulation curves suggest that the full range of species in the bay was considerably under-estimated. Additional species would most likely be detected at depths from 20–50 m, where sampling intensity was much lower than in shallower parts of the bay. Additional species are also likely to be small and rare; they will probably have unusual life habits and will probably be detected in bulk samples from soft substrata, from systematic sampling in cryptic habitats and from commensal associations. The consideration of dead shells in this survey helped us to recognize species that were rare or that colonize very specialized habitats. The probability of finding them alive within a reasonable time was low, with a reasonable number of samples, or without destructive sampling methods. Surveys of this type may help to identify areas of conservation importance, especially where living bivalves are only present in low numbers.

Key words: Mollusca, diversity, Red Sea, Indian Ocean, habitat, sampling intensity

Introduction

Most of the world's surface is sea, but most general works on biodiversity have concentrated on land areas (Williamson 1997; Gray 2000). This is not surprising for two reasons: (1) weak evidence suggests there are ten times as many multicellular terrestrial species as marine species (Williamson 1997; Reaka-Kudla 1997); (2) the study of marine biodiversity requires a much greater effort than is the case for land areas (Solbrig 1991).

Typically, biological diversity in marine environments is described on two scales, each based on a distinct type of data: Benthic ecologists sample small surfaces (up to a few m²) and restrict their analyses to living organisms (e.g. Kendall & Aschan 1993; Schlacher et al. 1998; Ellingsen 2001; Rumohr et al.

2001), but biogeographers and systematists pool data on species recorded from larger areas (up to several thousand km²) and integrate data from both live-collected animals and empty shells (e.g. Bouchet et al. 2002; Bieler & Mikkelsen 2004, Crame 2000a,b).

This study follows the second approach and provides data on a spatial scale that is also relevant to conservation policies. This is the scale of coastal bays, which cover tens to a few hundreds of km² (e.g. Bouchet et al. 2002). Research agendas for marine diversity should concentrate on such coastal regions, particularly in tropical and subtropical areas where species richness is potentially high and anthropogenic influences are great. Moreover, such coastal areas typically exhibit a wide variety of habitats such as hard rocky surfaces, kelp forests,

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seagrass beds, mangroves and coral reefs (Gray 1997).

Molluscs are the most diverse marine phylum and their diversity is particularly high in the tropical waters of the Indo-Pacific (Gosliner et al. 1996). Because of their widespread geographical distribution and relatively well-elaborated taxonomy, they are among the most useful taxonomic groups for investigating biodiversity patterns at local, regional and global scales (e.g. Thorson 1957; Stehli et al. 1967; Sanders 1968; Flessa & Jablonski 1996; Roy et al. 2000; Jablonski et al. 2000; Crame 2000a,b; Mikkelsen & Bieler 2000; Bouchet et al. 2002; Mackie et al. 2005). They are also considered to be an indicator group for the rapid assessment of coral reef diversity (Wells 1998). However, only very few studies on molluscan diversities so far considered factors like sampling strategies, literature records, habitats or life habits on species richness (e.g. Bouchet et al. 2002; Mikkelsen & Bieler 2004; Bieler & Mikkelsen 2004). Therefore, the purpose of this study is to combine the results from different sampling programs, including quantitative and qualitative surveys on hard and soft substrata and a few literature records, to estimate the species richness of bivalves in a single, coral-dominated, shallow-water bay in the northern Red Sea. Specifically, we want to answer the questions of how the observed species richness relates to sampling strategies, habitat variety, water depth covered, shell size considered, and the rarity and life habits of the respective species. We then discuss the influence of our results on estimates of bivalve diversity in the Red Sea and compare our results to local diversities from other tropical areas.

Material and methods

Study area

The Northern Bay of Safaga is a coral-dominated, shallow-water area measuring approximately 10 km from N–S and approximately 7 km from E–W. It exhibits a highly structured bottom topography extending down to more than 50 m water depth (Figure 1). The annual water temperature ranges between 21 and 29°C, salinity between 40 and 46 ‰, both without any obvious depth gradient due to complete water mixing. The tidal range is <1 m (Piller & Pervesler 1989). Terrigenous (thus nutrient) input occurs mainly along the coast and is due to fluvial transport during flash floods, local erosion of impure carbonate rocks and aeolian transport by the prevailing northerly winds (Piller & Mansour 1994). Water energy is relatively weak, but a complex current pattern influences facies develop-

ment (Piller & Pervesler 1989) and bottom facies and sedimentary facies generally show a good correspondence (Piller & Mansour 1990; Piller 1994).

Collecting history

In 1984, the Northern Bay of Safaga was chosen to study bottom types, sediments, burrows and selected groups of benthic organisms with considerable fossilization potential (including coralline red algae, foraminifera, corals, echinoids and molluscs) with respect to their palaeoecological significance (Piller & Pervesler 1989; see Zuschin & Oliver 2003a for summary of references). Four- to six-week field investigations were carried out in April/May 1986, November 1986, February 1987, and July/August 1987 and resulted in the basic mapping of bottom facies and description of sedimentary facies (Piller & Pervesler 1989; Piller & Mansour 1990). During the mapping of bottom facies (Piller & Pervesler 1989), numerous samples (mostly from soft substrata) were taken all over the bay and evaluated qualitatively for the present study. Three- to four-week field campaigns by the authors in October/November 1994, July/August 1995, May/June 1996 and March/April 1997 resulted in all quantitative samples from hard- and soft substrata and in most qualitative samples used for this study.

Sampling

From a methodological point of view this diversity study is based on three major sampling programs, which covered soft substrata and hard substrata and included both quantitative and qualitative samples, in a depth range from intertidal to 52 m. A total of 206 samples were evaluated and 18141 shells were studied in an area of approximately 75 km². About 10% (1821) of the shells could not be identified to the species level either because they were juveniles (mostly found in quantitative soft substrata samples) or because they belonged to species aggregates that could not be better identified in our quantitative field survey on hard substrata (e.g. Chamoidea, Ostreoidae). Excluding these 1821 shells of juveniles and species aggregates reduced the total number of samples available for this study to 193, because 13 samples from hard substrata contained no species-level data. Details on the quantitative importance and distribution patterns of juveniles and species aggregates are provided in Zuschin and Oliver (2003a).

All shells used for this study stem from the sea floor or from the uppermost 30 cm of the sediment, which is considered as the taphonomically active

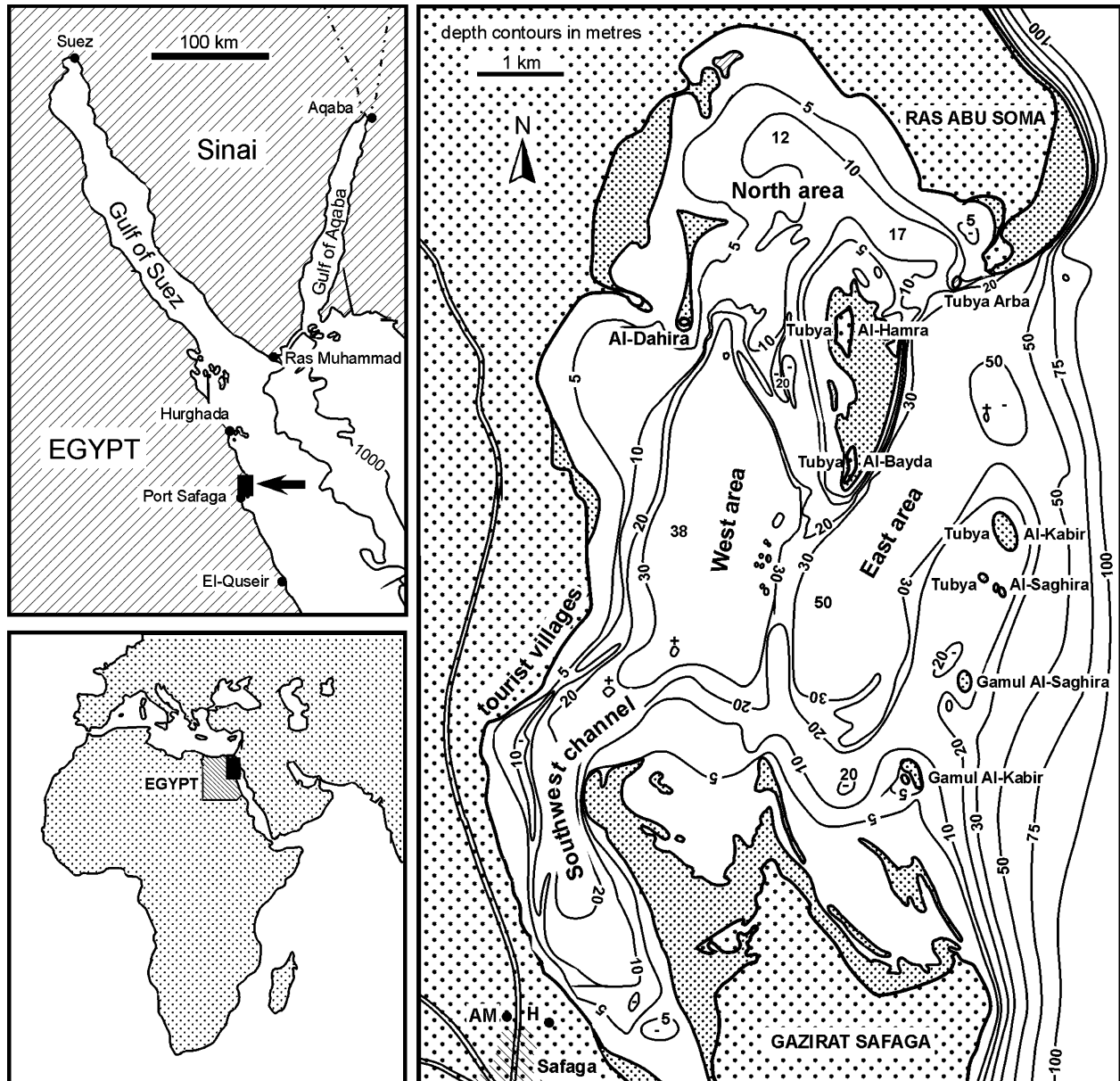


Figure 1. Location map and general bathymetry of the study area (after Piller & Pervesler 1989). Dense stippled fields in the right map are intertidal areas. AM = Aerial mast, H = "Safaga Hotel".

zone (Davies et al. 1989). This zone is sufficiently homogenized by continuous bioturbation and physical reworking, and actualistic studies suggest that in carbonate environments the majority of shells (especially the huge amount of juveniles) from this zone are young (mostly in the range of decades), although significantly older shells can occur (Kidwell et al. 2005). However, we sampled only the uppermost layers and certainly no Pleistocene fossils were inadvertently included in this study. The results of this study are therefore representative for the Recent Red Sea and appropriate for comparisons with any other shell collection from modern marine environments. It is also clear, however, that the results of

this study are not directly comparable to studies, which measure ecological diversity based on live-collected fauna.

For this diversity study, living and dead bivalves were pooled for all analyses. For hard substrata, separate data for live and dead fauna are available (Zuschin et al. 2000, 2001; Zuschin & Oliver 2003a). Due to time constraints, for soft substrata no attempt was made to differentiate between living and dead molluscs. Living bivalves, however, were extremely rare and based on the scarcity of articulated valves they are estimated to contribute far less than 1% to the total bivalve fauna (Zuschin & Hohenegger 1998).

Quantitative data from soft substrata samples. For the quantitative analysis of soft substrata molluscs, we studied 13 standardized bulk samples taken by scuba diving. All quantitatively studied sedimentary facies except the mangrove channel are represented by more than one sample (Table I), whose water depth ranges from shallow subtidal to 40 m (Figure 2). Most of these samples (six samples; 46%) come from a water depth of 10 m or less, two samples (15%) from 11–20 m, two samples (15%) from 21–30 m, and three samples (23%) from 31–40 m. No quantitative sediment samples from depths below 40 m were evaluated (Figure 2).

A steel cylinder (diameter 35 cm) was pushed into the sediment and the uppermost 30 cm, with a volume of 29 dm³, was collected into a 1 mm-mesh net. The sediment was air-dried and molluscs >2 cm were removed before splitting the samples using a modified sample splitter as described by Kennard and Smith (1961).

For more details on soft substrata samples see Zuschin and Hohenegger (1998) and Zuschin and Oliver (2003a).

Quantitative data from hard substrata. Different intertidal and subtidal hard substrata were sampled for bivalves at 74 localities in Safaga Bay with a 0.25 m² aluminium, square frame. The sampling sites were chosen to cover all major subtidal hard substrata (Table I) and the water depth of samples

ranges from intertidal to 40 m. Most transects (samples) were taken at depths of 10 m or less (37 transects; 50%), 25 transects (33; 8%) between 11 and 20 m, eight transects (10; 8%) between 21 and 30 m, and four transects (5.4%) between 31 and 40 m. No transects were laid at depths below 40 m (Figure 2).

At each locality, on such substrata, the location of the first frame was selected haphazardly by a diver throwing the frame from a few meters above the substratum. The subsequent frames were positioned contiguously along a line extending from that point. In mixed hard-substrata/loose-ground and/or soft-bottom habitats, frames were taken only from hard substratum. A mean of 4.4 m² (\pm 2.0) of seafloor was investigated per locality, with a range from 1–11 m². For more details on hard substrata samples see Zuschin et al. (2000, 2001) and Zuschin and Oliver (2003a).

Qualitative samples. During the initial mapping of bottom facies (Piller & Pervesler 1989), numerous samples (mostly from soft substrata) were taken all over the bay and these were evaluated qualitatively in the present study. Additionally, we unsystematically collected shells from close to most of our quantitative hard substrata stations and in the course of dives from around (mostly deeper-water) soft substrata stations. The species list of boring (endolithic) bivalves (Kleemann 1993) was treated as a qualita-

Table I. Number of samples, shells and species related to sampling strategies and bottom types in the Northern Bay of Safaga. The category "Safaga" contains the species list of boring (endolithic) bivalves (Kleemann 1993) and four specimens from our own sampling activity, for which no depth and habitat information was recorded. Total area sampled is approximately 75 km².

		No. samples	No. shells	No. Species
Soft bottoms (quantitative)	total	13	14132	148
	sand between coral patches	4	3893	80
	sand on reef slope	2	689	63
	muddy sand	2	1279	43
	mud	2	1629	29
	muddy sand with seagrass	1	4333	45
	sand with seagrass	1	2178	55
	mangrove channel	1	131	21
	total	74	1232	25
Hard substrata (quantitative)	reef flat	5	9	3
	reef slope	12	191	8
	coral carpets	44	816	22
	coral patches	3	55	8
	rocky intertidal	3	132	2
	subtidal rock bottom	7	29	10
	total	106	956	155
Qualitative samples	hard substrata	19	52	7
	soft substrata	38	483	75
	soft substrata near to hard substrata	47	392	90
	beached	1	1	1
	"Safaga"	1	28	28
	total	193	16320	243

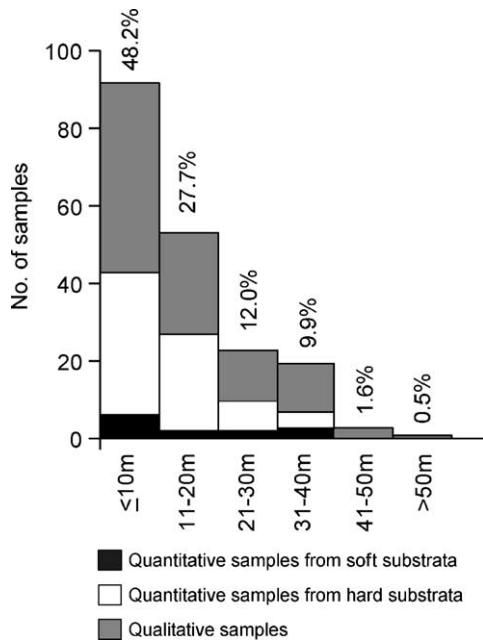


Figure 2. Sampling intensity (number and proportion of samples) in relation to water depth.

tive sample ("Safaga") for the purpose of our study and combined with four specimens from our own sampling activity, for which no depth and habitat information was recorded. A single specimen that was washed ashore is also included in this category (Table I). The water depth of qualitative samples ranges from intertidal to 52 m. Again, most of the qualitative samples (49 samples, 47.1%) were taken in depths shallower than 10 m; 26 samples (25%) were taken between 11 and 20 m, 13 samples (12.5%) between 21 and 30 m, 12 samples (11.5%) between 31 and 40 m, 3 samples (2.9%) between 41 and 50 m, and 1 sample (1%) from below 50 m. All samples taken below 40 m are qualitative (Figure 2).

Overlaps between quantitative and qualitative sampling strategies. Not all bivalved molluscs can be consistently identified to the species level during quantitative surveys of hard substrata because many taxa are byssally attached or cemented to a hard substratum and many species can only be identified based on the internal features of opened shells. This resulted in a group of taxa that could be identified only as species aggregates in the field. Most notably, these are *Tridacna* spp., *Chamoidea*, *Spondylidae*, *Ostreoidae*, and *Ptereria* spp. In the course of the quantitative hard substrata survey, however, we took selected samples of these taxonomic aggregates to identify the involved species. Nonetheless, the results of these identifications cannot be applied to the complete

data set of the quantitative hard substrata survey, and such selected samples of aggregates are treated here as qualitative samples.

Taxonomy

Of the 243 species of bivalves used in this study, 201 were already known from the Red Sea prior to our study (later on termed "known species"), but 42 are new records or new species (later on termed "new species") (Glover & Taylor 1997; Taylor & Glover 2000; Oliver & Zuschin 2000, 2001; Zuschin & Oliver 2003a; Taylor et al. 2005).

Two-hundred-and-eighteen species are figured and their taxonomic status discussed in Zuschin and Oliver (2003a). They include 198 species in the taxonomic sense (i.e. they are identified and named), and 20 recognizable taxonomic units (RTUs, also termed morphospecies or parataxonomic units, see Krell 2004), which were identified to the genus or family level only. The latter mostly (16 morphospecies) are considered as new species or new records for the Red Sea for the purpose of our study, and an effort was made to ensure that these RTUs represent species in a taxonomic sense. The 24 boring (endolithic) species are listed in Kleemann (1993). A single species (*Brechites* sp.) is no longer available to us.

From 16,320 shells included in this study, 98.7% were identified to the species level; 219 valves were identified to the genus or family level and represent the 20 recognizable taxonomic units (RTUs). The material of the present study is mostly stored at the Natural History Museum Vienna and at the National Museum of Wales in Cardiff.

Shell size

The maximum size (typically the anterior-posterior length, but sometimes the dorsal-ventral height) of each species (endolithic species excluded) from Safaga Bay was measured and log-transformed to normalize the size-frequency distribution, for which the mean, median and mode were calculated as standard measures of location (average values).

Life habits

The species found in Safaga Bay were classified into habitat tiers (epifaunal, infaunal, endobyssate, boring, commensal) and trophic guilds (suspension feeders, deposit feeders, chemoautotrophs, carnivores and zooxanthellates) according to their substrate relations and feeding strategies.

Analytical treatment

The number of shells was recorded for each species at each station. Species accumulation curves were computed using the program EstimateS (Colwell 2000), with 50 sample order randomizations without replacement. Samples are added to the analysis in random order and each sample is selected only once. By randomizing many times, the effect of sample order can be removed by averaging over randomizations, producing a smooth species accumulation curve (Colwell 2000).

We tested for significant differences in water depth, abundance, and shell-size between the 201 known species and the 42 new species using the non-parametric Kruskal-Wallis test. We tested for significant differences in life habits between known species and new species with cross tables and contingency analysis. The statistical analyses were

performed using the software package SPSS 10.0 (SPSS 1999).

Results

Diversity and sampling effort

A total of 16,320 shells from 193 samples represent 243 species of bivalves; the species are unevenly distributed among higher taxa. Among subclasses and orders, the Heterodonta and Veneroidea strongly dominate, respectively. Among superfamilies and families, the species are more evenly distributed. Eight superfamilies are present with 10 or more species; most important are the Tellinoidea, Veneroidea, and Mytiloidea. The richest families present are the Veneridae, Mytilidae, and Tellinidae, each with more than 20 species (Figure 3, see also Appendix).

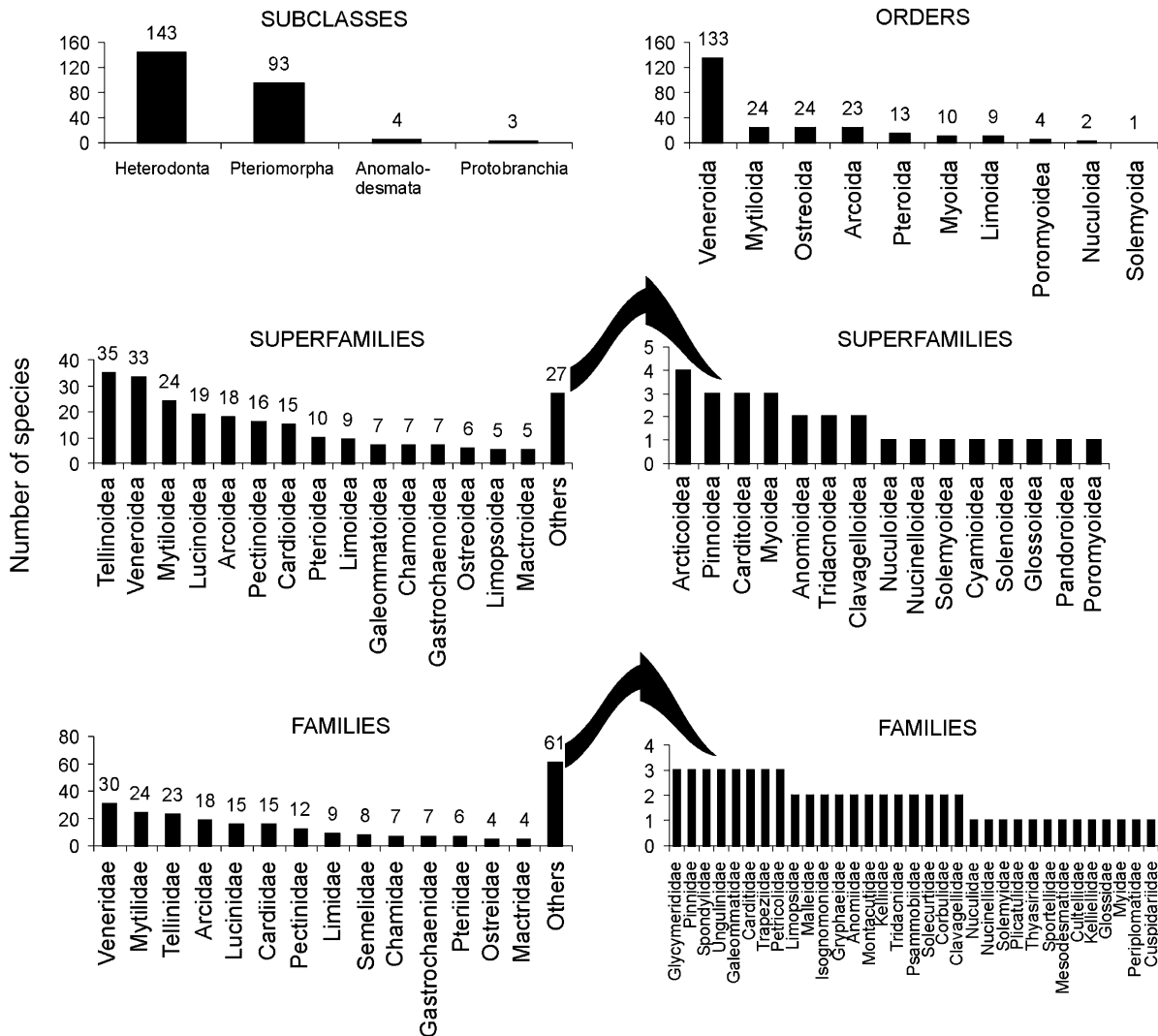


Figure 3. Species richness of higher taxa found in the Northern Bay of Safaga.

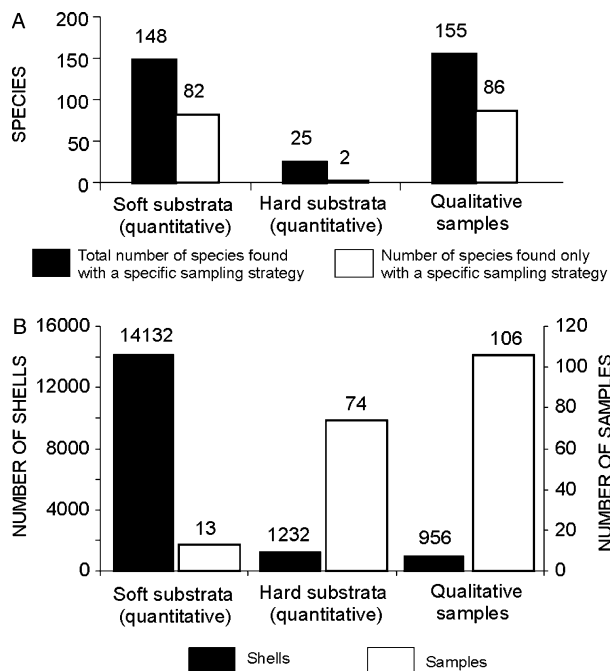


Figure 4. (A) Species numbers in relation to sampling strategies. (B) Species numbers in relation to sampling intensity.

Species numbers are also unevenly distributed among sampling strategies (Figure 4). The most species (155) were found in qualitative samples, which are characterized by the highest number of samples (106) and the lowest number of shells (956). The few quantitative samples from soft substrata (13) nonetheless yielded the highest number of shells (14,132) but fewer species (148) than qualitative samples. The high number of samples (74) from the quantitative hard substrata survey yielded very few shells (1,232) at the species level and also very few species (25) (Figure 4). The number of species found only with a particular sampling strategy was high for qualitative samples (86) and for quantitative samples from soft substrata (82), but low for quantitative samples from hard substrata (2) (Figure 4).

Species accumulation curves for all samples combined and for individual sampling strategies do not level off, indicating that the full range of species present was not captured (Figure 5). All samples combined yielded 243 species, but estimates range between 281 (Bootstrap) and 367 (Jack 2). The quantitative samples from soft substrata revealed 148 species, with estimates ranging from 168 (Bootstrap) to 197 (Jack 2). The quantitative samples from hard substrata revealed 25 species with estimates ranging from 29 (Bootstrap) to 40 (Jack 2). The qualitative samples yielded 155 species and the estimates ranged from 188 (Bootstrap) to 292 (Jack 2) (Figure 5).

The 243 species observed in Safaga Bay make up more than 54% of the total of bivalve species richness known from the Red Sea (Figure 6). Among the seven most species-rich superfamilies in Safaga Bay, the Arcoidea and Mytiloidea contained more than 70% of the species known from the Red Sea; the corresponding values in the Lucinoidea and Cardioidea were more than 60%, Tellinoidea and Veneroidea more than 50%. Only the Pectinoidea exhibited less than 50% of the known Red Sea species (Figure 6).

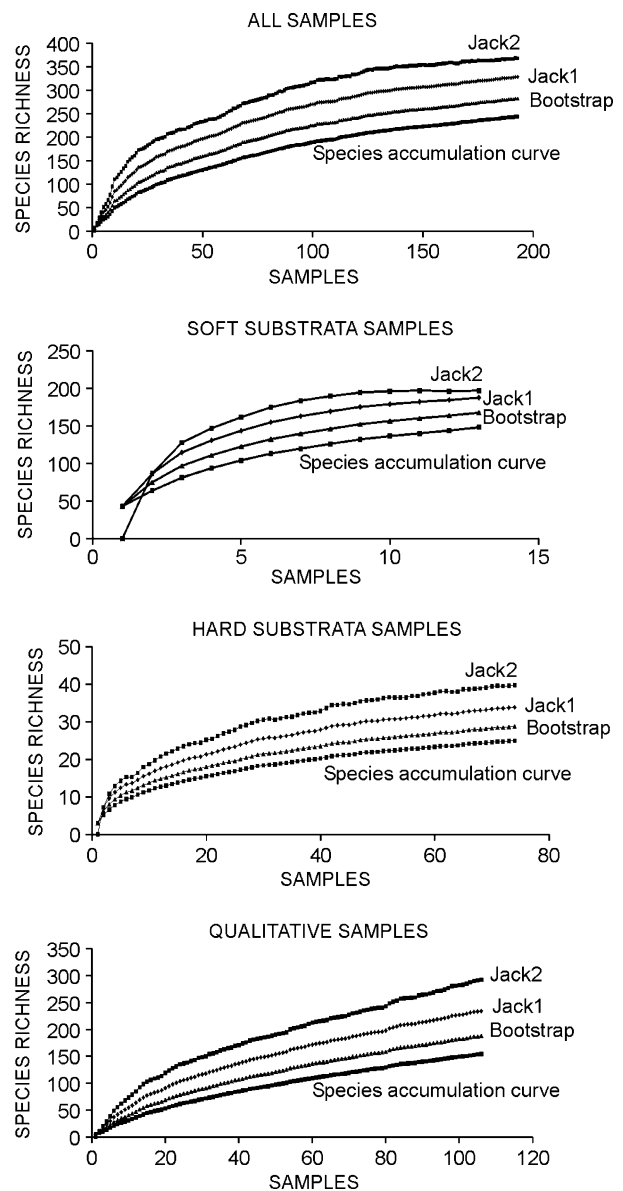


Figure 5. Species accumulation curves and estimates for species richness (Jack 1, Jack 2, Bootstrap) calculated with the program EstimateS (Colwell 2000) for the study area (all samples combined) and individual sampling strategies.

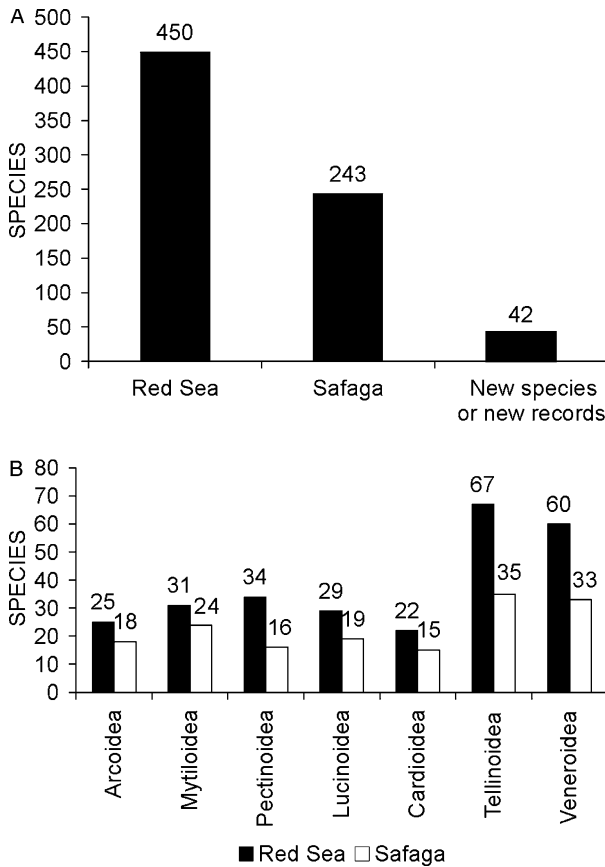


Figure 6. Bivalve species richness. (a) Number of new species or new records from our study in relation to the total species richness in Safaga and in the Red Sea. (b) Species richness of the seven most speciose superfamilies present in Safaga in comparison to the respective species numbers recorded for the Red Sea bivalve fauna.

Life habits

Most species (59.7%) found in Safaga Bay are epifaunal and infaunal suspension feeders, followed by the infaunal deposit feeders, boring suspension feeders, and infaunal chemoautotrophs. Only a few species are endobyssate or commensal suspension

feeders, epifaunal with zooxanthellae (2 species; 0.8%), or infaunal carnivores (1 species; 0.4%) (Figure 7). Most epifaunal species are byssally attached crevice dwellers, byssally attached surface dwellers, or cemented to hard substrata. Only a very few species are byssally attached on the surface of soft substrata or belong to the free-lying epifauna. About three-quarters of the infaunal species are shallow infaunal; only one-quarter is deep infaunal (Table II).

Rarity

Most species collected in Safaga Bay are neither abundant nor frequent (Figure 8). More than 50% of the species (122) are represented in our collection by 5 valves or less, 69 species (28.4%) are singletons (represented by single specimens), and 19 species (7.8%) are doubletons (represented by only 2 specimens). Only 31 species (12.8%) are represented by more than 100 shells (Figure 8A), and the most abundant species, *Cardiolucina semperiana*, makes up 20.3% of all valves. Eighty-five species (35%) are uniques (restricted to a single valve or shell) and 45 species (18.5%) are duplicates (present in only 2 samples). Only 22 species (9.1%) occur in more than 10 samples (Figure 8B), and the most frequent species, *Pedum spondyloideum*, occurred in 56 samples (29% of all samples). Only 12 bivalve families (from a total of 47 families present) contribute more than 1% each to the total number of shells counted. Together, these 12 families make up 93.6% of all valves. By far the most abundant family is the Lucinidae, followed by the Tellinidae and the Veneridae (Table III, see also Appendix).

Shell size

The maximum size of the 219 species (boring species excluded) collected in Safaga Bay ranges from 2–300 mm, but most species are rather small.

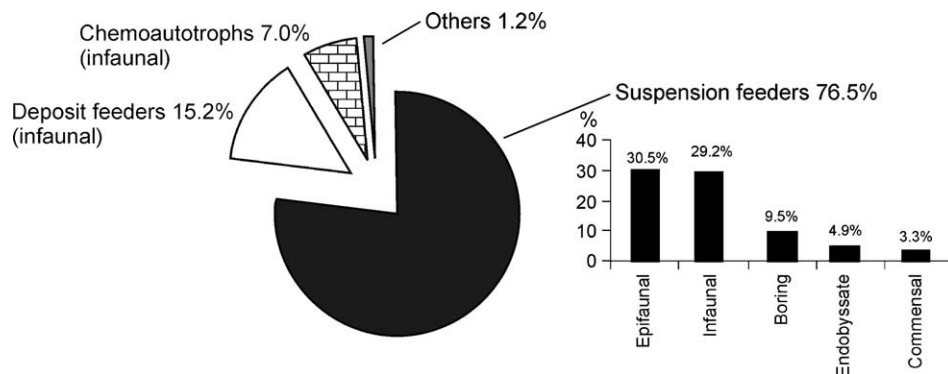


Figure 7. Life habits (feeding strategies and substrate relations) of the bivalve species found in our study.

Table II. Habitat tiers of the 243 bivalve species found in the Northern Bay of Safaga.

Habitat tiers	n	%
Epifaunal	74	30.5
bysally attached on hard substrata	19	7.8
cemented epifauna	17	7.0
crevice dweller/cryptic	32	13.2
bysally attached on soft substrata	4	1.6
free-lying epifauna	2	0.8
Boring	23	9.5
Infaunal	126	51.9
shallow infaunal	94	38.7
deep infaunal	32	13.2
Endobysate	12	4.9
Commensal	8	3.3

The mean value is 36 mm, the median 25 mm, and the mode only 17 mm. The two largest size classes are 21.6–30.6 mm and 30.7–43.4 mm. Nearly half (45.2%) of the species are smaller than 21.5 mm and 27.4% of the species are larger than 43.5 mm (Figure 9).

Water depth

The water depth covered in this study ranges from intertidal to 52 m. Most species (almost two-thirds), however, were found in depths shallower than 10 m. The mean minimum water depth in which a species was collected is 13.4 m (median 6 m, mode 0.5 m) (Figure 10A). The respective mean maximum water

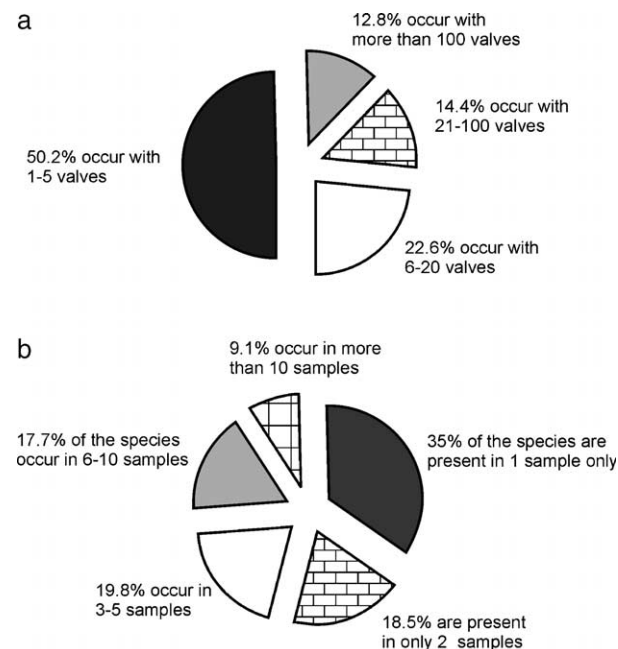


Figure 8. Rarity of molluscs at Safaga. (a) The number of species in four abundance categories. (b) The number of species in five occurrence categories.

Table III. The abundance and species richness of the 12 bivalve families (from a total of 47 families present) that contribute more than 1% each to the total number of shells counted (compare also Appendix).

Family	No. valves	% valves	No. species
Lucinidae	6345	38.9	15
Tellinidae	1781	10.9	23
Veneridae	1690	10.4	30
Cardiidae	1006	6.2	15
Corbulidae	855	5.2	2
Pectinidae	720	4.4	12
Glycymerididae	709	4.3	3
Mytilidae	696	4.3	24
Carditidae	564	3.5	3
Arcidae	437	2.7	18
Semelidae	301	1.8	8
Limopsidae	170	1.0	2

depth is 28.5 m (median 30 m, mode 40 m) (Figure 10B).

New species and new records

New species or new records for the Red Sea are significantly less abundant, significantly smaller, and occurred in significantly greater water depth than those species already known prior to our study (Tables IV and V). The life habits of new species/new records for the Red Sea are significantly different ($\chi^2 = 33.555$, $df = 7$, $p < 0.0001$) from those of known forms. A new species or new record for the Red Sea is most likely to be an infaunal chemoautotroph, a boring (endolithic) or commen-

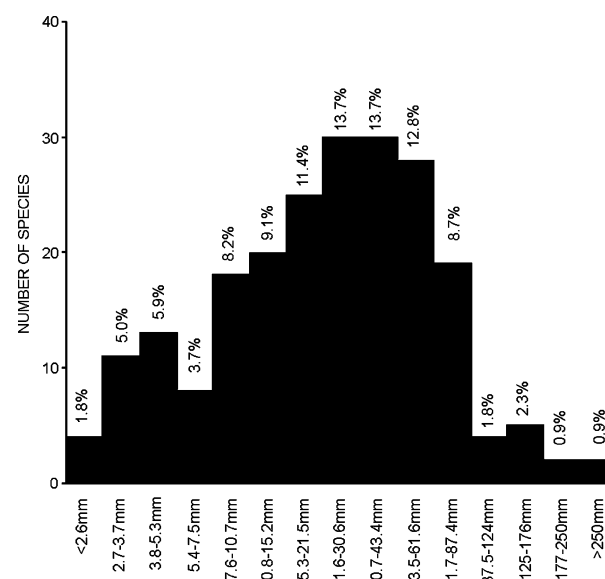


Figure 9. Size distribution of 219 bivalve species (endolithic bivalves not included) found in the Northern Bay of Safaga, based on the maximum diameter recorded for each species. The 15 size classes have equivalent log-transformed intervals.

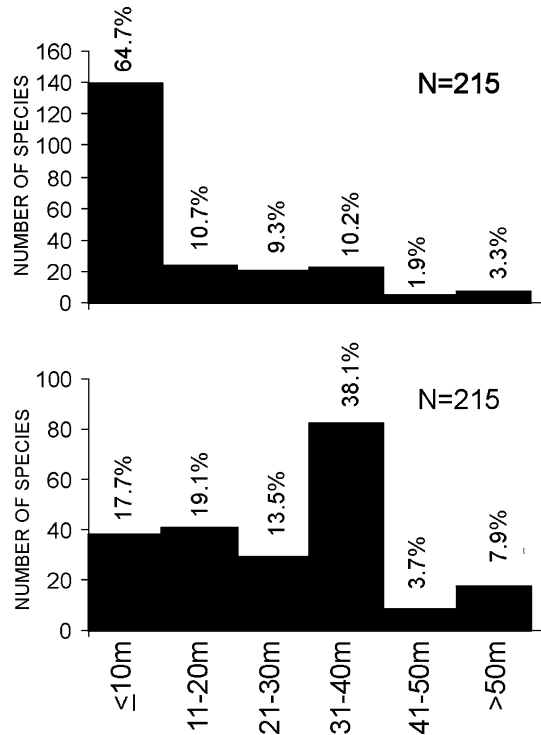


Figure 10. The water depth for 215 bivalve species (no depth data for boring species and four additional species) collected in the Bay of Safaga. (a) The minimum water depth in which a species was collected. (b) The maximum water depth in which a species was collected.

sal suspension feeder as indicated by high standardized residuals in the cross table (Table VI). By far the most new species, which are new or new records (28) were found in quantitative soft substrata samples. Sixteen new species or new records were found in qualitative samples and none in quantitative samples from hard substrata. There is only minor overlap between sampling strategies: the qualitative and quantitative samples from soft substrata had only two new species/new records in common.

Table IV. Average abundance, size and minimum water depth in which a species was found in Safaga. Values are shown for new species or new records for the Red Sea and for those species already known prior to our study.

	Abundance	Size (mm)	water depth (m)
known species			
mean	74.4	39.6	11.9
median	7	17	0.5
mode	1	29	6
new species			
mean	32.5	12.6	21.9
median	2	3.5	10
mode	1	5.8	19

Table V. Non-parametric Kruskal-Wallis test for differences in water depth, abundance and shell-size between known species and new species.

	Chi-Square	df	Significance
Water depth	24.700	1	<0.001
Abundance	6.137	1	0.013
Size	32.596	1	<0.001

Discussion

Bivalve species richness in the Bay of Safaga in comparison to other regions

With 243 recorded bivalve species (and estimates ranging between 281 and 367) in an area of about 75 km², the species richness in the Northern Bay of Safaga is the highest reported for coastal areas of comparable size. In the Indian River Lagoon (central eastern Florida coast) an intense survey over several years yielded 156 bivalve species (Mikkelsen et al. 1995). For the shallow-water coral-dominated bays around Mahé, Seychelles, with a distinctly narrower depth range, 115 bivalve species are reported (Taylor 1968). The value for a much larger area with a similar depth range but distinctly lower sampling intensity, on 16 coastal and offshore reefs of Port Sudan is 76 bivalve species (Mastaller 1978). Sheppard (1984) reported 99 species in the Chagos Archipelago, which has a comparable area and depth range but was probably sampled less intensively. For a distinctly lower depth range and habitat variety, but comparable surface area around the island Rodrigues (Indian Ocean) 109 bivalve species are reported (Oliver et al. 2004).

Bouchet et al. (2002) reported 519 bivalve species for the west coast of New Caledonia, but that study differs in several aspects from ours: the 295 km² area covered is about 4 times larger. Moreover, the water depth covered (intertidal to 120 m) is much larger than in our study (intertidal to 52 m). The authors also applied sampling techniques not possible in our study (e.g. suction sampling, dredging, systematically breaking hard substrata). Finally, the New Caledonia study devoted special attention to sampling parasitic and commensal molluscs from various invertebrates, and smaller shell sizes were considered (>0.37 mm in New Caledonia versus >1 mm in our study). For the Florida Keys, 389 species are reported from a much larger area (about 28,000 km²), greater depth range and certainly a higher sampling intensity including dredging (Mikkelsen & Bieler 2000; Bieler & Mikkelsen 2004). Similarly, the Southern Gulf of Thailand contained 229 species from a similar depth range (0–50 m) but much larger area (about 10,000 km²), covering mostly soft sediment, including estuaries and man-

Table VI. Cross table of life habits (substrate relations and feeding strategies) for known species and new species. Fields with high standardized residuals contribute most to the significant result of the Chi-square statistics.

	Deposit infaunal	Chemoautotrophs infaunal	Suspension epifauna	Suspension infauna	Suspension boring	Suspension en- dobyssate	Suspension commensal	Others
Known species								
counts	32	11	64	63	13	12	3	3
expected	30.6	14.1	59.6	58.7	19.0	9.9	6.6	2.5
counts standardized residuals	0.3	-0.8	0.6	0.6	-1.4	0.7	-1.4	0.3
New species								
counts	5	6	8	8	10	0	5	0
expected	6.4	2.9	12.4	12.3	4.0	2.1	1.4	0.5
counts standardized residuals	-0.6	1.8	-1.3	-1.2	3.0	-1.4	3.1	-0.7
Total								
counts	37	17	72	71	23	12	8	3

groves, but little if any coral habitats (Swennen et al. 2001).

Factors responsible for the high bivalve species richness in Safaga

We relate the high species richness in Safaga Bay primarily to habitat variety, sampling intensity and to the subsequent taxonomic efforts. In the Northern Bay of Saga the habitat variety is great for the relatively small area and it was intensively studied with quantitative and qualitative samples (Table I). The great sampling intensity also enabled us to find many rare species; consider that nearly half of the species occurred in only one or two samples, and more than half were found with 5 valves or less (compare Figure 8). We made a great effort to include not only the large shells, which are typically studied by shell collectors and in rapid assessment surveys (e.g. Wells 1998), but also small shells measuring a few millimeters only (for a detailed discussion of this point see Bouchet et al. 2002). We covered a relatively large depth range (intertidal to 52 m) and the taxonomic effort was very high in this study.

Similarly, Bouchet et al. (2002) reported more than 2700 marine mollusc species (519 bivalves species) from a larger area in New Caledonia, the authors related this extraordinary biodiversity to a massive collecting and sorting effort of an area with high habitat heterogeneity.

Pooling of living and dead bivalves for diversity studies

On hard substrata in Safaga Bay living and dead bivalves are certainly mostly autochthonous, because

they are typically byssally attached or cemented to the sea floor. Most of the bivalves found were alive, and dead shells reflected the taxonomic composition of the living assemblage very well. Differences between abundances and distribution patterns of living and dead shells can be mostly related to postmortem overgrowth of dead shells by corals (Zuschin et al. 2000, compare also Zuschin & Oliver 2003b). For this reason, pooling of living and dead bivalves does not overestimate the species richness on hard substrata.

On soft substrata, living molluscs were extremely rare in our samples and probably contribute far less than 1% to the total mollusc content (Zuschin & Hohenegger 1998). Therefore, the studied mollusc associations are representative of death assemblages. We believe that the death assemblages involve the local fauna because they correlate so strongly with sedimentary facies. Moreover, there is no sedimentological evidence for considerable transport that would produce allochthonous assemblages. Finally, the ecological properties of the associations match the sedimentary facies so well, that the species distributions are very unlikely a consequence of the behaviour of shells as sedimentary particles (Zuschin & Hohenegger 1998).

Such time-averaged death assemblages typically retain a strong signal of the species' original rank orders (Kidwell 2001) but overemphasize the species richness of any single census of the local live community (Staff & Powell 1988; Kidwell 2002a). Nevertheless, it is useful to include empty shells into diversity studies for various reasons: (1) in our case it would have been impossible to perform a diversity study solely based on living shells from soft substrata because living molluscs were so rare in sediments

and the resources for sampling were limited. Studying death assemblages is instructive especially in tropical soft sediments, where only few living bivalves are usually present in quantitative samples; (2) most species were so rare that it is very unlikely we would have found living individuals within a reasonable time. In fact such rare species can only be detected alive by extremely intensive and long-term studies of living animals (for review see Kidwell 2002b); and (3) many species occupy very specialized habitats, which are difficult to sample for living species. Including empty shells, therefore, helped not only to save time and money but is also comparatively environmental friendly. For these and similar reasons, dead shells are routinely included in diversity studies of molluscs on local and regional scales (e.g. Mikkelsen & Bieler 2000; Bieler & Mikkelsen 2004; Bouchet et al. 2002; Warwick & Light 2002). Large-scale comparisons of regional bivalve faunas (e.g. Crame 2000a,b) from around the world are mainly based on dead shells. Bouchet et al. (2002) for example, specifically raised the point that empty shells are biodiversity indicators. This points to the difficulty of estimating the real magnitude of species richness for taxa that leave no post mortem remains (e.g. polychaetes).

Implications for bivalve diversity in the Red Sea and other subtropical-tropical seas

When our molluscan survey began, the first assessment of the Red Sea bivalve fauna was 411 species (Oliver 1992). The latest checklist recorded 421 species (Dekker & Orlin 2000). A further 19 taxa (mostly not determined to the species level) are figured and discussed in Zuschin and Oliver (2003a); together with the species listed by Kleemann (1993), this brings the known total to 450 species.

The approximately 75 km² area we sampled yielded 243 species, representing 54% of the total bivalve fauna known from the Red Sea (including also bathyal species). Despite this high percentage, species accumulation curves suggest that the full range of species in the bay was far from fully captured (Figure 5). Our data also suggest that many shallow-water bivalves remain to be detected in Safaga Bay because more than 75% of our samples were taken at depths shallower than 20 m, and samples from 20–50 m are progressively under-represented (compare Figure 2). In our opinion, it is safe to assume that this depth range (20–50m) is undersampled in the whole Red Sea and probably also in many other regions of the Indo-Pacific. This interpretation is also supported by new species or new records (endolithic species not included) we

found: these species occurred in significantly greater water depth than known species and therefore reflect lower sampling intensities in depths beyond the reach of snorklers and at the lower limit of typical Scuba dives. Note also that the environmentally heterogeneous 50–300 m depth range is also not well sampled in the Red Sea, but shows a very high bivalve diversity (von Rützen-Kositzkau 1999, Grill & Zuschin 2001). Relatively few additional samples can yield many new species here. In contrast, the depth range from 300–1900 m is environmentally uniform and sampling intensity is comparatively high (von Rützen-Kositzkau 1999; Grill & Zuschin 2001).

Water depth and habitat variety are not the only factors that influence the potential number of new species in Safaga Bay. Additional species are also likely to be small, to occur with relatively few shells, and to have extraordinary life habits. Among the sampling strategies applied so far, a new species is most likely to be detected in bulk samples from soft substrata (i.e. our quantitative samples). Very small shells not easily found lying on the sea floor can be extracted here. Shells lying on the seafloor were mostly considered in our qualitative samples and in the quantitative samples on hard substrata. Note also that we only minimally sampled cryptic habitats and omitted invertebrates for commensal or parasitic species. Such strategies would certainly strongly increase the number of species detected in Safaga and in the Red Sea.

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Appendix

List of bivalve superfamilies and families collected in Safaga. Taxa are shown in their systematic order with number of shells and number of species.

Superfamily	Family	No. valves	No. Species
Nuculoidea	Nuculidae	67	1
Nucinelloidea	Nucinellidae	108	1
Solemyoidea	Solemyidae	1	1
Arcoidea	Arcidae	437	18
Limopsoidea	Limopsidae	170	2
	Glycymerididae	709	3
Mytiloidea	Mytilidae	696	24
Pinnoidea	Pinnidae	56	3
Pterioidea	Pteriidae	46	6
	Malleidae	16	2
	Isognomonidae	43	2
Pectinoidea	Pectinidae	720	12

APPENDIX (*Continued*)

Superfamily	Family	No. valves	No. Species
	Spondylidae	35	3
	Plicatulidae	25	1
Limoidea	Limoidea	161	9
Ostreoidea	Ostreidae	137	4
	Gryphaeidae	15	2
Anomioidea	Anomiidae	8	2
Lucinoidea	Lucinidae	6345	15
	Thyasiridae	1	1
	Ungulinidae	78	3
Galeommatoidea	Galeommatidae	7	3
	Montacutidae	2	2
	Kelliidae	2	2
Cyamioidea	Sportellidae	7	1
Chamoidea	Chamidae	106	7
Carditoidea	Carditidae	564	3
Cardioidea	Cardiidae	1006	15
Tridacnoidea	Tridacnidae	13	2
Mactroidea	Mactridae	8	4
	Mesodesmatidae	1	1
Solenoidea	Cultellidae	1	1
Tellinoidea	Tellinidae	1781	23
	Semelidae	301	8
	Psammobiidae	33	2
	Solecurtidae	34	2
Arcticoidea	Trapeziidae	5	3
	Kelliellidae	7	1
Glossoidea	Glossidae	2	1
Veneroidea	Veneridae	1690	30
	Petricolidae	9	3
Myoidea	Myidae	1	1
	Corbulidae	855	2
Gastrochaenoidea	Gastrochaenidae	7	7
Pandoroidea	Periplomatidae	1	1
	Cuspidariidae	1	1
Clavagelloidea	Clavagellidae	2	2
		16320	243